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Published in:
Bulletin of the Geological Society of Denmark

Publication date:
2018

Document version
Publisher's PDF, also known as Version of record

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Cuny, G. & Stemmerik, L. 2018. New fossil fish microremains from the Upper Carboniferous of eastern North Greenland. © 2018 by Bulletin of the Geological Society of Denmark, vol. 66, pp. 47-60. ISSN 2245-7070. (www.2dgf.dk/publikationer/bulletin).

The Moscovian of eastern North Greenland has yielded an assemblage dominated by teeth and dermal denticles of chondrichthyans with rarer teeth of actinopterygians. The rather poor preservation of the material precludes precise identification but the following taxa have been recorded: *Adamantina foliacea, Bransonella* spp., *Denaea* sp., *"Stemmatias" simplex, Lagarodus specularis,* Actinopterygii indet., as well as teeth probably belonging to new genera of Heslerodidae, ?Protacrodontidae and Hybodontiformes. This fauna appears therefore quite endemic. The abundance of *Bransonella* and durophagous chondrichthyans is in accordance with the shallow marine depositional environment. The record of a ?protacrodontid is possibly the youngest one for this taxon.

Keywords: Greenland, Carboniferous, Moscovian, Foldedal Formation, sharks, euchondrocephals.

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Received 27 January 2017
Accepted in revised form
27 October 2017
Published online
6 March 2018

In Greenland, marine Carboniferous sediments are restricted to the Wandel Sea Basin of eastern North Greenland where shallow marine siliciclastics, carbonates and $CaSO_4$ evaporites of Moscovian to Gzhelian age unconformably overlie Lower Carboniferous (Visean) non-marine sediments and older rocks (Stemmerik & Håkansson 1989). The Upper Carboniferous sediments belong to the Kap Jungersen and Foldedal Formations of the Mallemuk Mountain Group and are part of a widely distributed succession of warm-water shelf sediments that were deposited along the northern margin of Pangea during the late Carboniferous and earliest Permian (Stemmerik 2000). During the time of deposition, North Greenland was located at around 35°N in a region characterized by warm and arid climate. The marine biota in the shelf carbonates belong to the late Palaeozoic warm-water chloroforam association recorded from Arctic Canada in the west across North Greenland, Svalbard and the Barents Shelf to Arctic Russia in the east (e.g. Beauchamp 1994; Stemmerik 2000). Records of fossil sharks from this vast warm-water shelf succession are few. Four taxa have been reported from North Greenland (Bendix-Almgreen 1976) and recently the occurrence of *Lagarodus* was expanded to also include Svalbard (Cuny *et al.* 2016). The only records of fossil sharks from the Moscovian of Arctic Russia are from Novaya Zemlya and North Timan and include dermal denticles of ctenacanth, hybodont and neoselachian sharks, *"Stemmatias"*-like denticles, teeth of *Cooleyella* sp. and fragments of "bradyodont" toothplates (Ivanov 1999).

This paper describes a fish fauna from a carbonate bed in an otherwise shale-dominated interval in the lower part of the Foldedal Formation at Kap Jungersen, southern Amdrup Land (Fig. 1). The interval occurs in the lower part of sequence S5 in section 6 in Davydov *et al.* (2001, fig. 3). The well-exposed coastal cliff sections at Kap Jungersen are dated by fusulinids and correlated to the Russian type sections (Davydov *et al.* 2001). The fish fauna is from sediments belonging to the lower Moscovian (Kashirian) *Citrinoides paraozawai* zone of Davydov *et al.* (2001). Altogether around 100 chondrichthyan teeth and denticles and more than 50 actinopterygian microremains were recovered. The new material thus adds to our understanding of the fish fauna and diversity of the northern warm-water province during the late Carboniferous.

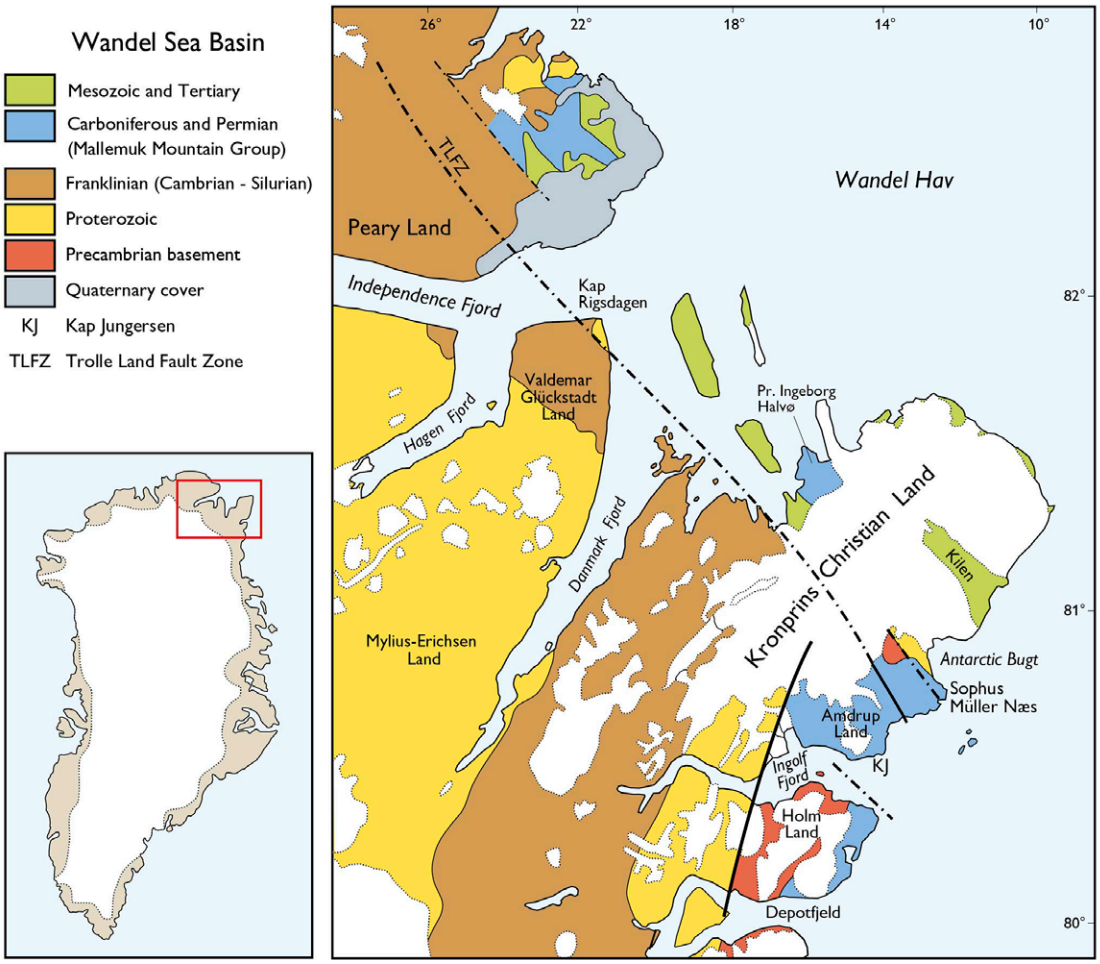

Fig. 1. Map of eastern North Greenland showing the distribution of marine Upper Palaeozoic sediments in the Wandel Sea Basin and location of the study locality (KJ).

Methods

The microremains were retrieved by dissolving approximately 250 g of limestone in 10% acetic acid, which resulted in *c.* 90 g of non-carbonate material. This material was sieved using 1 mm and 63 μm sieves and the fraction <1 mm and >63 μm was density separated; the light fraction, approximately 10 g, was then sorted for fish microremains using a microscope.

The systematic scheme used here follows Ginter *et al.* (2010). The use of the term 'root' in the following descriptions does not imply direct homology with the root of the teeth of other gnathostomes (Underwood *et al.* 2015).

All the specimens are housed at the Natural History Museum of Denmark, University of Copenhagen (abbreviation: MGUH).

Systematic palaeontology

Class Chondrichthyes Huxley 1880

Subclass Elasmobranchii Bonaparte 1838

Family Jalodontidae Ginter, Hairapetian & Klug 2002

Genus *Adamantina* Bendix-Almgreen 1993
***Adamantina foliacea* Ivanov 1999**
Fig. 2Q-T

Material. One tooth, NHMD 189710.

Description. NHMD 189710 is a tricuspid tooth measuring 1 mm mesio-distally. The three cusps are damaged, but the main cusp was probably a little higher than the mesial and distal ones. The bases of the cusps are fused. The crown is quite asymmetric, the mesial

(?) cusp being broader than the distal(?) one. The ornamentation of the labial face is chevron-shaped, whereas the lingual one displays faint and scarce ridges on the side of the cusps, but their central part is smooth.

The root is short and projected lingually, its basal face being perpendicular to the crown. There is a large central foramen at its lingual extremity. Additional foramina are present mainly at the base of the crown lingually. There is a pair of well-developed labiobasal projections, one on each side of the central cusp of the crown, separated by a basolabial depression.

Comparisons. The tricuspid crown and chevron-shaped labial ornamentation of NHMD 189710 are reminiscent of teeth of *Bransonella,* but the absence of a central labial basal tubercle, replaced by a pair of labiobasal projections, allows easy separation of these two kinds

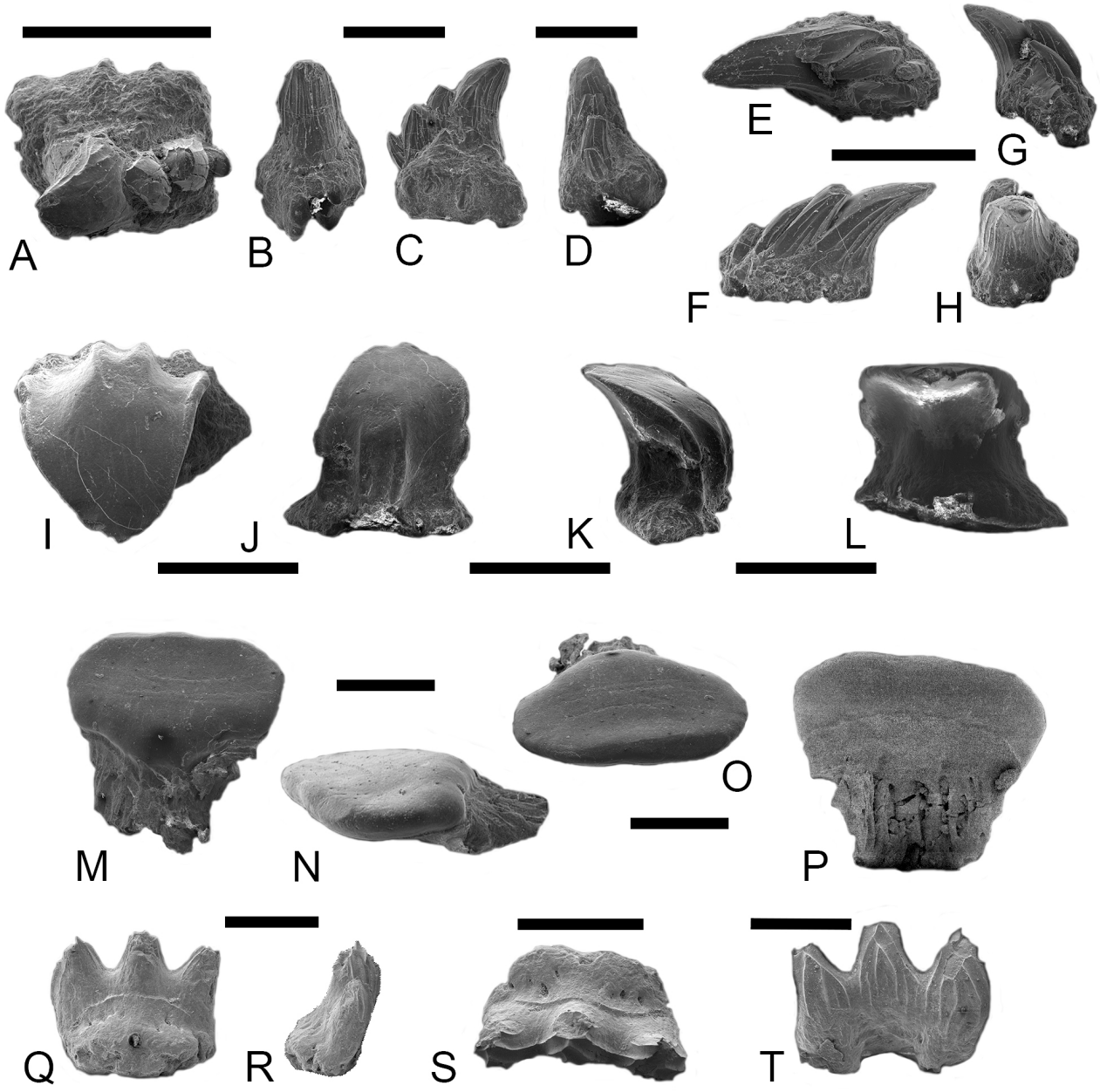

Fig. 2. A–H: *"Stemmatias" simplex*. **A–D**: NHMD 189706; **A**: apical view. **B**: anterior view. **C**: lateral view. **D**: posterior view. **E–H**: NHMD 189707; **E**: apical view. **F**: lateral view. **G**: posterior view. **H**: anterior view. **I–P**: dermal denticles of indeterminate chondrichthyans. **I–L**: NHMD 189708; **I**: apical view. **J**: anterior view. **K**: lateral view. **L**: posterior view. **M–P**: NHMD 189709; **M**: anterior view. **N**: lateral view. **O**: apical view. **P**: posterior view. **Q–T**: *Adamantina foliacea,* NHMD 189710; **Q** lingual view. **R**: mesial or distal view. **S**: apical view. **T**: labial view. All scale bars represent 500 μm.

of teeth. A similar chevron-shaped ornamentation, as well as the presence of two labiobasal projections separated by a depression, is also encountered in jalodontids (Ivanov 1999; Ivanov *et al.* 2012). Many characters (a short root, the presence of a deep and wide labio-basal depression with prominent rounded tubercles, cusps labio-lingually compressed with their base fused, sub-equal in height and width, showing sub-parallel axes and ornamented by rare weak ridges on their lingual side) suggest that NHMD 189710 is better attributed to *Adamantina foliacea* (Ivanov 1999). *A. benedictae* differs from NHMD 189710 by a spirally curved ornamentation and central cusp shorter than the lateral ones (Bendix-Almgreen 1993).

Superorder Xenacanthimorpha Nelson 1976

Order Bransonelliformes Hampe & Ivanov 2007

Genus *Bransonella* Harlton 1933
***Bransonella* spp.**
Fig. 3

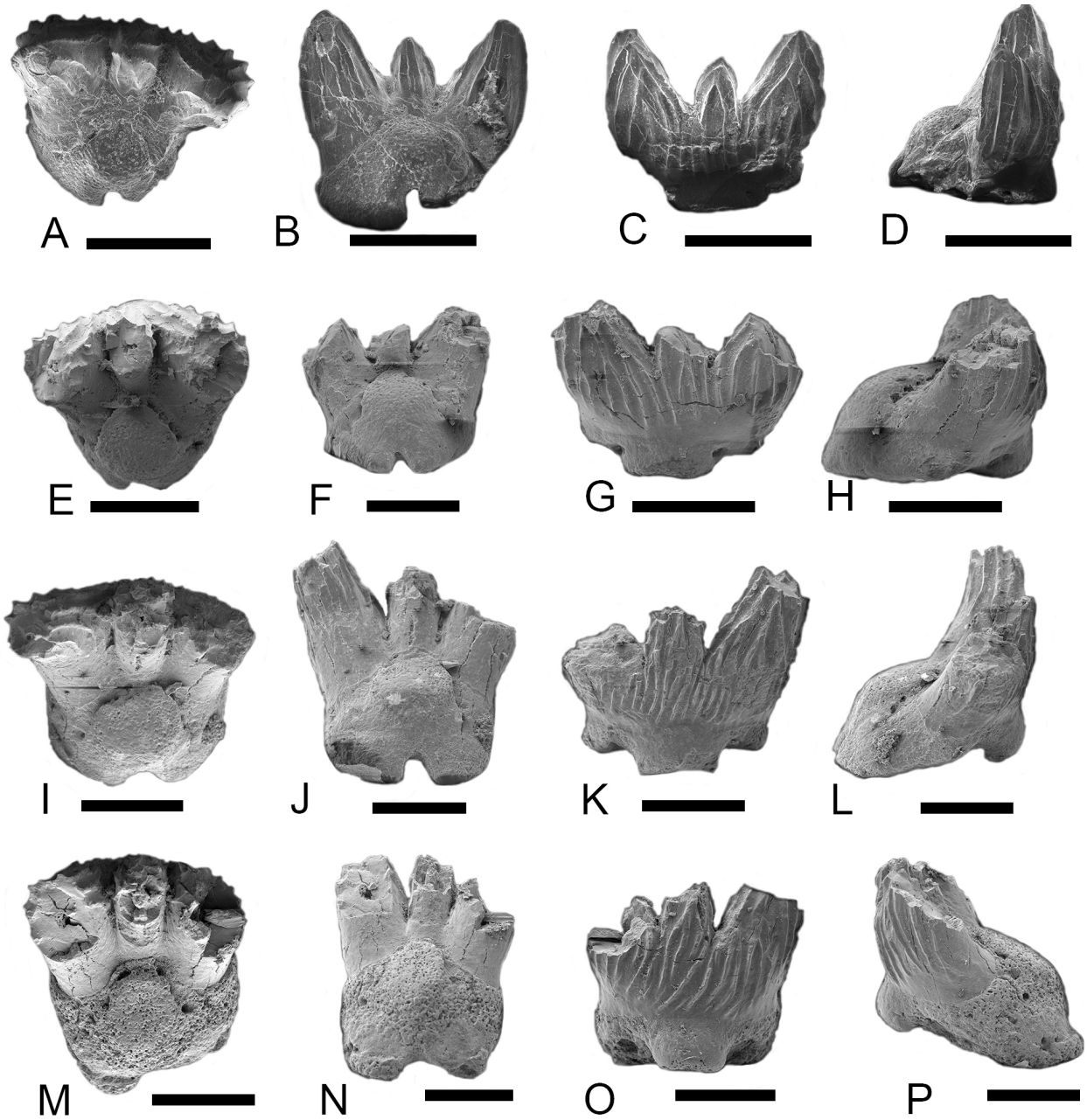

Fig. 3. *Bransonella* spp. **A–D**: NHMD 189711. **E–H**: NHMD 189713. **I–L**: NHMD 189715. **M–P**: NHMD 189716. **A**, **E**, **I**, **M**: apical views. **B**, **F**, **J**, **N**: lingual views. **C**, **G**, **K**, **O**: labial views. **D**, **H**, **L**, **P**: mesial or distal views. All scale bars represent 500 μm.

Material. Six teeth, NHMD 189711 to NHMD 189716, and approximately 20 fragments.

Description. The crown of the best preserved specimen (NHMD 189711, Fig. 3A–D) is tricuspid and measures 1 mm mesio-distally. The mesial and distal cusps are twice the size of the intermediate one. The cross-section of the base of the mesial and distal cusps are almost circular, whereas the one of the intermediate cusp is more compressed mesio-distally. On the labial face, the ridges ornamenting the cusps anastomose to form chevrons. Some less well-preserved teeth, especially NHMD 189712 and NHMD 189716 (Fig. 3M–P), show an ornamentation denser and more oblique than that of NHMD 189711. The ornamentation on the lingual face is less developed than the one on the labial face with only two ridges on each cusp in NHMD 189711, whereas the lingual face of NHMD 189716 appears to be completely smooth. In addition, all three cusps possess well-developed cutting edges.

The root is projected lingually, perpendicularly to the crown. It shows a well-developed orolingual button, circular in outline. It covers most of the lingual surface of the root, except in NHMD 189711 where it is reduced in size and does not contact any of the cusps. On the lingual extremity of the root there is a notch corresponding to the opening of an unroofed vascular foramen. There are some additional foramina scattered irregularly on the surface of the root both labially and lingually. A basal tubercle is present on the labial margin, often with a foramen opening mesially and distally to it.

Comparisons. The following features allow these teeth to be attributed to the genus *Bransonella* (Ginter *et al.* 2010): The tricuspid crown has an intermediate cusp smaller than the mesial and distal ones, its labial ornamentation is chevron-shaped, the lingually extended root has a large orolingual button, and there are a labial basal tubercle and labial foramina. The intermediate cusp in the Greenland specimens appears smaller than that of the older (Tournaisian) teeth of *Bransonella* sp. described from Arctic Russia (Ivanov 1999). The Greenland teeth also differ from the ones of *B. tribula* by the lack of a pentagonal orolingual button elongated labio-lingually (Elliott & Hodnett 2013). The Greenland teeth are, however, quite disparate and may represent several species. When preserved, their rather low intermediate cusp and the presence in some teeth of a dense and strongly sigmoidal labial ornamentation are reminiscent of *B. lingulata*, but their orolingual button does not always reach the lingual rim of the root and some teeth show ridges on the lingual side of the crown. These two latter characters are more reminiscent of *B. nebraskensis* (Ivanov & Ginter 1996; Johnson & Thayer 2009). Based on the morphology of its orolingual button and its smooth lingual crown, NHMD 189716 is the only tooth that would be better attributed to *B. lingulata* than to *B. nebraskensis,* but the labial ornamentation of the crown is more similar to that of *B. tribula* than to that of *B. lingulata*. In addition, the small lingual button of NHMD 189711, not in contact with the crown, is reminiscent of *B. tridentata*, but as this species is only known from a single, incomplete specimen, comparisons are difficult (Harlton 1933; Zidek 1973; Johnson 1984; Johnson 2005; Johnson & Thayer 2009).

Superorder Cladodontomorphi Ginter, Hampe & Duffin 2010

Order Symmoriiformes Zangerl 1981

Family Falcatidae Zangerl 1990

Genus *Denaea* Pruvost 1922
***Denaea* sp.**
Fig. 4A–H

Material. Two teeth, NHMD 189717 and NHMD 189718.

Description. NHMD 189717 measures 1.2 mm mesio-distally, whereas NHMD 189718 is larger with a mesio-distal length of 2 mm. The crown consists of a main cusp strongly arched lingually and flanked by two pairs of diverging lateral cusplets. The outer cusplets are larger than the inner ones and have a rounded cross-section. The main cusp is biconvex, with the lingual side more convex than the labial one. The labial face is ornamented by 8 to 13 non-anastomosing ridges and the lingual face by 14 to 16 similar ridges, some of which are restricted to the lower part of the cusp. The main cusp and lateral cusplets are connected by a faint lateral carina.

The root is projected lingually, showing a triangular outline in apical view. The orolingual ridge is elongated mesio-distally and displays a shallow concavity in its central part, separating a mesial and a distal button. The labial outline of the root shows a convexity at the level of the main cusp. One foramen corresponding to the main vascular canal opens on the lingual rim and there are smaller foramina irregularly distributed all over the root.

Comparisons. NHMD 189717 and 189718 are quite similar to the teeth of *Squatinactis,* except that they are more densely ornamented and that the labial convexity at the base of the main cusp is not as well developed (Ivanov 1996; Ginter *et al.* 2010). The fact that cusp and cusplets

are connected by a faint lateral carina could suggest that NHMD 189717 and 189718 belong to a ctenacanthiform rather than to a symmoriiform (Ginter *et al.* 2010). However, as pointed out by M. Ginter and A. Ivanov during the review process of this manuscript, faint carina between the cusps are quite often observed in teeth of *Denaea* (Ginter *et al.* 2015). NHMD 189717 and 189718 also share a similar rounded cross-section of the cusps with *Denaea*. In addition, teeth of *Denaea* display roots with weakly developed articulation devices and an orolingual ridge almost split in two by the opening of the main basal canal. Moreover, their outline in apical view is similar to that of NHMD 189717 and 189718 (Ginter *et al.* 2015). The quite robust cusps of the two teeth from Greenland are reminiscent of the teeth attributed to *Denaea* sp. by Ginter *et al.* (2015).

Symmoriiformes incertae sedis

***"Stemmatias" simplex* (St. John & Worthen 1875)**
Fig. 2A–H

Material. Two denticles, NHMD 189706 and NHMD 189707.

Description. NHMD 189706 consists of four crowns forming a whorl over a fused base. The crowns decrease regularly in size posteriorly and are arched anteriorly. They are compressed antero-posteriorly. Their anterior faces are ornamented with numerous irregular ridges, whereas the posterior faces are almost smooth. The base is not very well preserved and shows a bulbous shape. It is almost as high as the main crown and is wider than the base of the crowns. Anteriorly, just under the base of the crowns, there is a row of foramina which fades posteriorly.

NHMD 189706 is very similar to NHMD 189707, except that the four crowns are not as well-aligned antero-posteriorly and the base appears less deep (Fig. 2E–H).

Comparisons. Specimens very similar to NHMD 189706 and 189707 were described from the Late Devonian and Late Carboniferous of Arctic Russia (Ivanov 1999), the Permian of Russia (Ivanov & Lebedev 2014) and the Late Devonian/Early Carboniferous of New Mexico (Ivanov & Lucas 2011). The latter specimens show a shallower base than the Greenland specimens, whereas the ones from Arctic Russia display a badly preserved base, making comparisons difficult. Ivanov (1999), Ivanov & Lucas (2011) and Ivanov & Lebedev (2014) attributed all these specimens to the genus *"Stemmatias"* and interpreted them as being buccopharyngeal denticles of Symmoriiformes. A similar single 'coxcomb' variety was attributed to the species *"Stemmatias" simplex* by Williams (2001). Similar buccopharyngeal denticles were also described *in situ* in several Symmoriiformes: *Cobelodus aculeatus* (Zangerl & Case 1976), *Stethacanthus* cf. *altonensis* (Zidek 1993) and *Stethacanthus (Akmonistion) zangerli* (Coates & Sequeira 2001). Koot *et al.* (2013) described similar specimens from the Permian of Oman but attributed them to *Gunnellodus bellistriatus* and interpreted them as buccopharyngeal denticles of Hybodontiformes, mostly because Symmoriiformes teeth were not recovered from the Permian of Oman. There is little morphological reason to separate *"Stemmatias" simplex* from *Gunnellodus bellistriatus* at genus level, and as *Stemmatias* Hay 1899 has priority over *Gunnellodus* Wilimovsky 1954, we refer our specimens as *"Stemmatias" simplex* buccopharyngeal denticles.

Zidek (1993) noted that pharyngeal whorls of denticles possess a thicker base in *Cobelodus* than in *Stethacanthus,* which might suggest than NHMD 189706 and 189707 belong to two different taxa.

Order Ctenacanthiformes Glickman 1964

Family Heslerodidae Maisey 2010

Heslerodidae indet.
Fig. 4I–P

Material. Two teeth, NHMD 189719 and NHMD 189720, and approximately 50 fragments.

Description. NHMD 189720 measures 1.8 mm mesio-distally, whereas NHMD 189719 is larger, measuring 3.2 mm mesio-distally with one of the extremities of the tooth lacking. The crown consists of a main cusp flanked by three pairs of lateral cusplets for NHMD 189719 and four pairs for NHMD 189720. The main cusp has a weakly convex labial face and a strongly convex lingual face. The labial face is ornamented with a few ridges of variable length, whereas the lingual ornamentation is denser, made of non-rectilinear ridges of variable length. In NHMD 189720 there are two ridges that anastomose to form a single ridge in the upper part of the labial face of the cusp, with a short ridge in between the two branches of the main ridge. The main cusp shows well-developed cutting edges. In NHMD 189719 only one of the lateral cusplets is partially preserved (Fig. 4J–K). In NHMD 189720 the outer pair of cusplets is the largest, the second pair the second largest, whereas the first and third pairs are the smallest (Fig. 4N–O). The outer pair was probably about half the height of the main cusp. The ornamentation of the labial faces of the cusplets is less dense than that of the lingual faces.

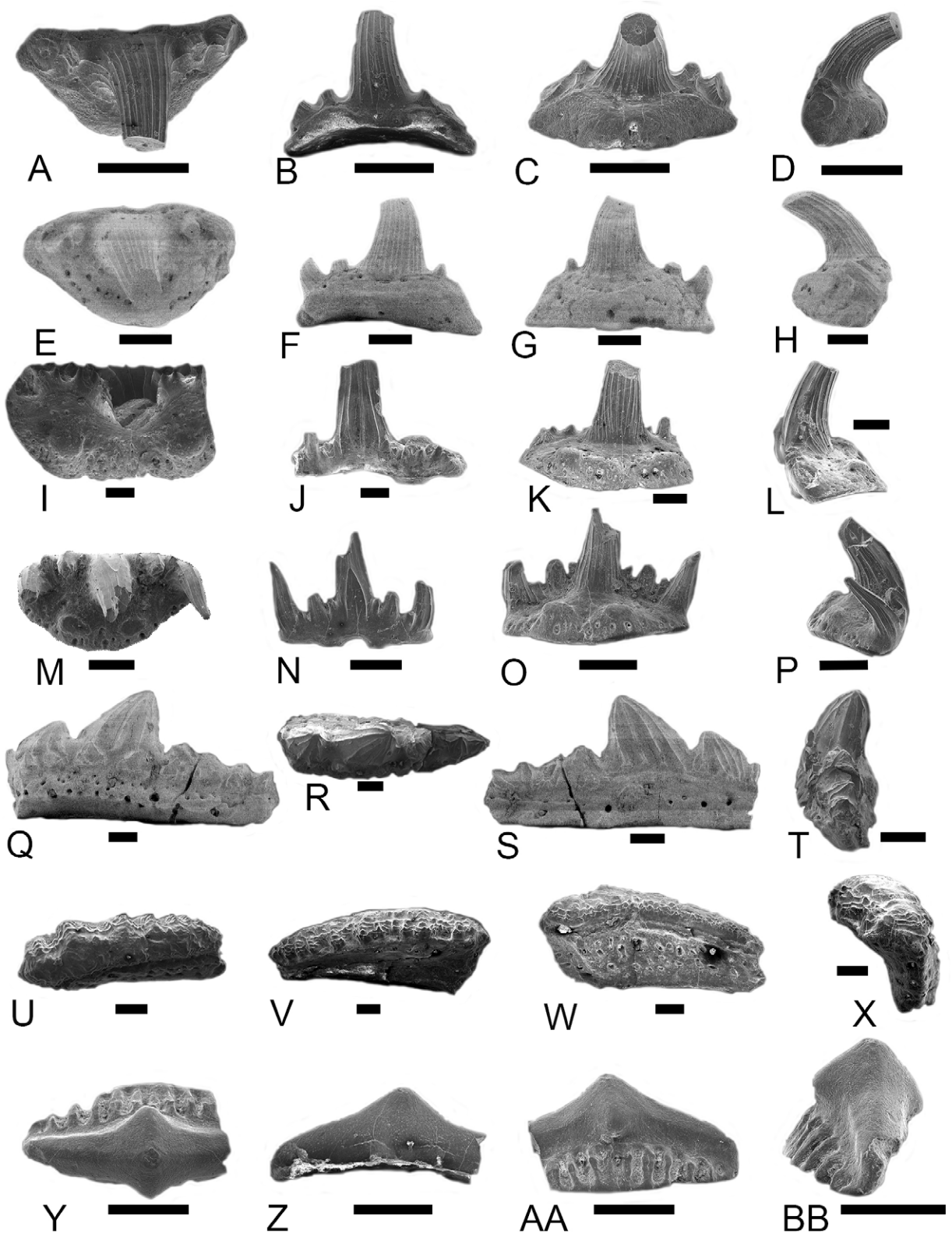

Fig. 4. A–H: Falcatidae indet. **A–D**: NHMD 189717. **E–H**: NHMD 189718. **A**, **E**: apical views. **B**, **F**: labial views. **C**, **G**: lingual views. **D**, **H**: mesial or distal views. **I–P**: ?Heslerodidae indet. **I–L**: NHMD 189719. **M–P**: NHMD 189720. **I**, **M**: apical views. **J**, **N**: labial views. **K**, **O**: lingual views. **L**, **P**: mesial or distal views. **Q–X**: Protacrodontidae indet. **Q–T**: anterior tooth NHMD 189721; **Q**: labial view. **R**: apical view. **S**: lingual view. **T**: distal view. **U–X**: posterior tooth NHMD 189722; **U**: apical view. **V**: labial view. **W**: lingual view. **X**: mesial view. **Y–BB**: Hybodontiformes indet. NHMD 189723; **Y**: apical view. **Z**: labial view. **AA**: lingual view. **BB**: mesial or distal view. All scale bars represent 500 μm.

The root is shallow and projected lingually, perpendicularly to the crown. In apical view it shows an almost quadrangular outline in NHMD 189719, but it is more semi-circular in NHMD 189720. There is a pair of well-separated orolingual buttons and labiobasal projections, one on each side of the main cusp of the crown. The orolingual buttons are almost circular in apical view. The root shows many foramina scattered over the whole surface, although they concentrate on its lingual margin. There are two paired enlarged foramina between the orolingual buttons in NHMD 189719 and a single one in NHMD 189720.

Comparisons. NHMD 189719 and NHMD 189720 differ from NHMD 189717 and NHMD 189718 by an ornamentation less dense on the labial side of the main cusp and a shallower root, not triangular in apical outline. The orolingual buttons are also clearly separated from each other, whereas this is not the case in NHMD 189717 and NHMD 189718. The presence of two separate orolingual buttons and two basolabial projections on each side of the main cusp suggests that NHMD 189719 and NHMD 189720 are closely related to the clade grouping *Kaibabvenator, Nanoskalme, Glickmanius* and *Heslerodus* as defined by Hodnett *et al.* (2012), although the orolingual buttons are not always completely separated in the teeth of *Heslerodus* (Ginter 2002). The presence of the same characters in the teeth of *"Ctenacanthus" costellatus* strongly suggests that this taxon also belongs to the same monophyletic group (Ivanov & Lebedev 2014). NHMD 189719 appears indeed quite similar to a fragmentary tooth from the Viséan of Derbyshire attributed to *"Ctenacanthus" costellatus* by Ginter *et al.* (2015), although it lacks a well-developed basolabial depression at the level of the main cusp. The lack of such a depression in NHMD 189719 and NHMD 189720 indicates that they are probably closer to *Kaibabvenator* + *Nanoskalme* than to *Glickmanius* + *Heslerodus* + *"Ctenacanthus" costellatus*.

Cohort Euselachii Hay 1902

Superfamily Protacrodontoidea Zangerl 1981

Family Protacrodontidae Cappetta, Duffin & Zidek 1993

?Protacrodontidae indet.
Fig. 4Q–X

Material. Two teeth, NHMD 189721 and NHMD 189722, and approximately 10 fragments.

Description. There are two different morphotypes of protacrodont teeth in the material. The first is represented by NHMD 189721 (Fig. 4Q–T) which measures 3.9 mm mesio-distally but is broken mesially. The crown shows a main cusp oriented distally, flanked by at least one mesial cusplet and three distal ones. The mesial cusplet is larger than the distal ones, giving the crown a marked asymmetric aspect. The main cusp and the mesial cusplet are ornamented by three to five ridges reaching the apices on the labial and lingual faces. There are one to two ridges on the distal cusplets on each face. The ridges ornamenting the mesial and distal cusplets are more irregular than those on the main cusp. They bifurcate basally and join together, forming a reticulate ornamentation at the base of the crown. A longitudinal crest, forming moderately developed carinae, joins all cusp and cusplets together. At the base of the labial face there is a row of nine small accessory labial cusplets.

The root is half the height of the crown and is separated from the latter by a moderately developed groove. Foramina of various sizes are scattered on the lingual and labial sides of the root. On the labial side, the larger foramina are positioned at the base of the root and can be unroofed basally, forming short grooves. The basal part of the lingual side is devoid of foramina and the larger ones are concentrated on the middle part of the face. The root is slightly inclined lingually.

The second morphotype, NHMD 189722 (Fig. 4U-X), is very asymmetric and 4.3 mm long mesio-distally. There are eight very low cusp and cusplets. The main cusp is flanked by one mesial cusplet and six distal ones. There are one or two well-developed labial nodes in front of each cusp and cusplet. The ornamentation of the crown is complex, made of fine, reticulated ridges with a mesio-distal main orientation and restricted to the lower part of the crown. In apical view the ornamentation forms irregular, concentric rings around the crown. The labial part of the crown overhangs the root. Lingually, the root is separated from the crown by a well-defined groove. The labial face of the root is concave in mesial or distal view, whereas the lingual face is straight under the crown. Foramina of variable sizes are scattered on the upper two-thirds of the root.

Comparisons. NHMD 189721 is reminiscent of teeth of *Sphenacanthus*, but in the latter labial accessory cusplets are generally lacking at the level of the main cusp (Soler-Gijón 1997; Ginter *et al.* 2010) and the teeth are more symmetric, except for some teeth of *S. carbonarius* (Ginter *et al.* 2010, fig. 94A). However, in the latter species the lingual projection of the root is more developed and the labial foramina tend to form a horizontal row (Soler-Gijón 1997; Ginter 2016). As

noted by Ginter *et al.* (2010), it is almost impossible to separate isolated teeth of protacrodonts from those of Palaeozoic hybodonts, and as a convention teeth from the Devonian have generally been attributed to protacrodonts, whereas Carboniferous teeth are more often attributed to hybodonts. However, NHMD 189721 shares features with teeth of *Deihim* such as a similar root vascularization, the presence of a row of accessory labial cusplets and a reticulate ornamentation at the base of the crown. The main difference to the latter genus is that the root appears less projected lingually and the base of the crown is almost flat and not as convex as in the teeth of *Deihim*, without diverging cusplets (Ginter *et al.* 2002; Roelofs *et al.* 2016). A tooth from the Devonian of Morocco attributed to cf. *Deihim mansureae* by Ginter *et al.* (2002, plate 6 I–K) shows completely fused cusps and a complex reticulated ornamentation, at least on the lingual face, which is quite similar to what can be seen on NHMD 189722. A reticulated ornamentation at the base of the crown has also been observed in teeth of *Protacrodus* sp. from the Early Carboniferous of Iran (Habibi & Ginter 2011, pl. 2B) as well as in the teeth of a Protacrodontidae? indet. from the Tournaisian of China, which also share with the Greenland specimens a highly asymmetric crown (Ginter & Sun 2007). Several Devonian protacrodontids also display a reticulated ornamentation at the base of the crown (Long & Hairapetian 2000; Ginter & Sun 2007; Roelofs *et al.* 2015). Hence, the presence of a row of labial accessory cusplets and reticulate ornamentation at the base of the crown lead us to attribute NHMD 189722 and NHMD 189721 to a protacrodontid rather than to a hybodont shark. The morphology of NHMD 189722 is also reminiscent of non-symphysial teeth of Eugeneodontiformes, but to the authors' best knowledge a reticulated ornamentation at the base of the crown is unknown among this order. If we are correct, this would extend the stratigraphic range of the protacrodonts to the Middle Pennsylvanian; they are currently considered to disappear in the Early Carboniferous (Ginter *et al.* 2010).

Order Hybodontiformes Patterson 1966

Hybodontiformes indet.
Fig. 4Y–BB

Material. One tooth, NHMD 189723.

Description. The crown is elongated mesio-distally, devoid of ornamentation, with a blunt main cusp. At the base of the main cusp there is a well-developed labial and lingual peg. The root is compressed labio-lingually and projected lingually. On the lingual face there is a series of nine furrows, with a foramen opening in the upper part of each furrow. As the mesial or distal part of the tooth is lacking, the total number of furrows was at least eleven, depending on whether the tooth was asymmetric or not. There is a row of large foramina in the uppermost part of the labial face of the root.

Comparisons. The root is of euselachian type according to Ginter *et al.* (2010). Its morphology, compressed labio-lingually, inclined lingually with well-developed furrows on the lingual face, is reminiscent of what can be observed in the enchondrocephalian *Cristatodens sigmoidalis* and the hybodont *Cassisodus margaritae* from the Tournaisian of China (Ginter & Sun 2007). However, the apparent lack of tubular dentine in the crown does not favour a relationships of NHMD 189723 to the Euchondrocephali. It is closer to *Cassisodus* and the Hybodontiformes, although its crown morphology is much simpler than in the latter genus. They share, however, the presence of a labial and lingual peg at the base of the main cusp, a character also found in other Palaeozoic Hybodontiformes such as *Omanoselache, Reesodus* and *Teresodus* (Koot *et al.* 2013). Furrows on the lingual side of the root are, however, not as well developed in these three taxa as in NHMD 189723. The latter therefore probably represents a new taxon closely allied to *Cassisodus*, but more material is necessary to test this hypothesis.

Elasmobranchii *incertae sedis*

Dermal denticles
Fig. 2I–P

Material. Two denticles, NHMD 189708 and NHMD 189709.

Description. NHMD 189708 is 0.7 mm high. Its crown is leaf-shaped and arched caudally. It shows two well-developed carinae that reach the apex of the crown, and two parallel ridges delimiting a mesial platform with a slightly concave surface that stops at the level of the caudal flexure. The subcrown is smooth. The pedicle is truncate (Johns *et al.* 1997) with at least six canal openings on its side.

The crown of NHMD 189709 is set almost horizontally, with a slightly concave surface. It is ovoid in shape, smooth, 1.8 mm long and 0.5 mm thick. Its anterior face shows a well-developed mesial protrusion. The subcrown is smooth with a well-developed halo. The pedicle is badly preserved and projected anteriorly. The anterior face presents two rows of canal openings. The subpedicle shows a series of furrows,

although this is likely to be an artefact due to post-mortem wear.

Comparisons. The shape of the crown of NHMD 189709 and its nearly horizontal position is reminiscent of the paragenus *Glabrisubcorona* Johns, Barnes & Orchard 1997 from the Late Triassic of Canada. However, its pedicle is much more projected anteriorly than in the latter. The presence of a double row of foramina openings on the pedicle is very unusual.

Subclass Euchondrocephali Lund & Grogan 1997

Order indet.

Family Lagarodontidae Lebedev 2008

Genus *Lagarodus* Jaekel 1898
***Lagarodus specularis* (Trautschold 1874)**
Fig. 5

Material. One tooth, NHMD 189724.

Description. This tooth is strongly arched and asymmetric, with the reduced mesial part of the cusp perpendicular to the distal part, forming a transversely elongated tubercle. It measures 12 mm mesio-distally, 6 mm labio-lingually and is 5 mm at its maximum height. The crown is quadrangular in apical view, the mesial extremity being slightly wider than the distal one. The apical surface shows a dense network of circular depressions corresponding to the opening of the dentinal canals of the tubular dentine (orthotrabeculine). The labial and lingual faces of the crown are ornamented by irregular ridges parallel to each other and running mesio-distally. The labial ornamentation is better developed than the lingual one. The labial face overhangs the root and is separated from the latter by a constriction.

The root is rhomboid in outline in basal view and is not projected lingually. It displays small foramina scattered over all faces except the basal one. There is a tendency for the foramina to be larger on the distal part than on the mesial part.

Comparisons. The following features allow identification of this tooth as the *angustus* morphotype of *Lagarodus specularis* (Lebedev 2008): The mesial part of the tooth is strongly reduced with its surface perpendicular to that of the distal one, the central tubercle is transversely elongated, and the ornamentation at the base of the crown is made of irregular and parallel

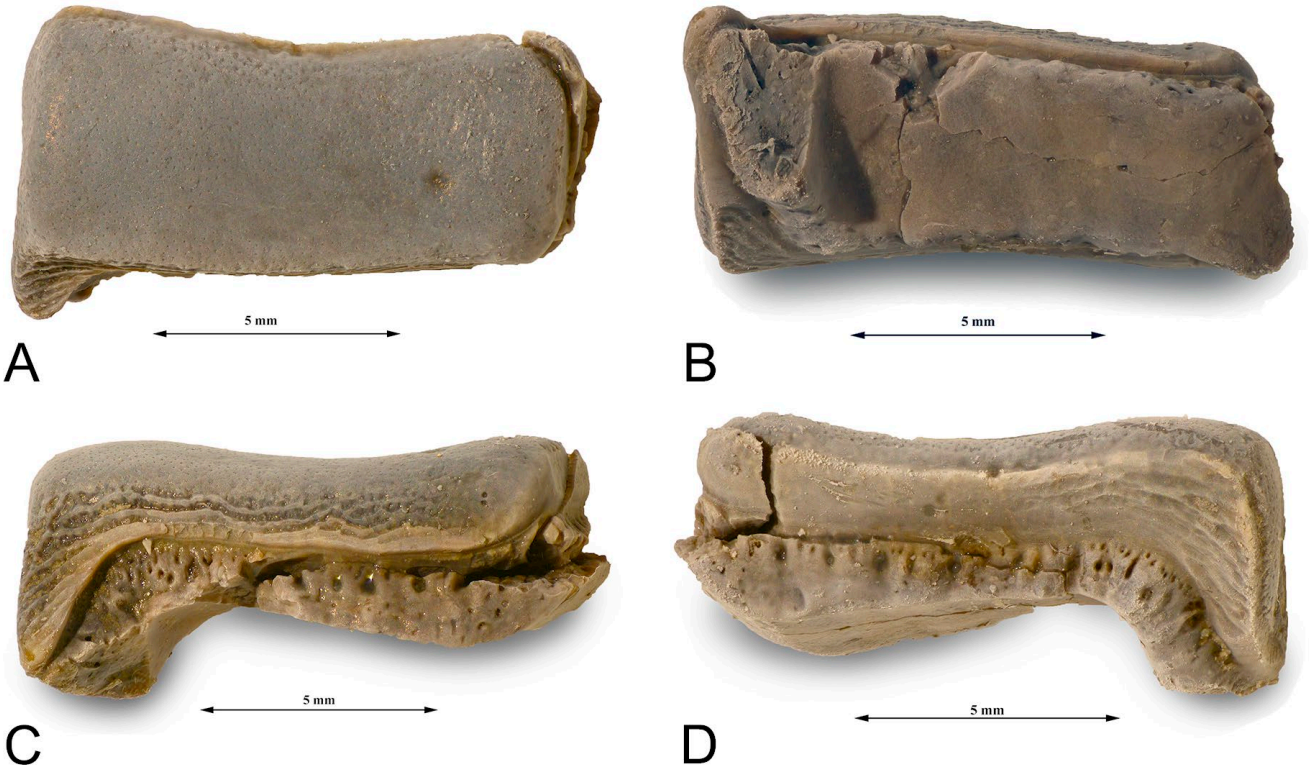

Fig. 5. *Lagarodus specularis,* NHMD 189724; **A**: apical view. **B**: basal view. **C**: labial view. **D**: lingual view.

mesio-distal ridges. The tooth therefore represents a parasymphysial tooth. Bendix-Almgreen (1975) described another parasymphysial tooth he attributed to *Lagarodus* sp. from the Upper Carboniferous of Amdrup Land. The latter is broken and more worn than the present specimen, but it shows no difference to it and is likely to belong to the same species.

It should be noted, however, that Cuny *et al.* (2016) recently suggested that a second species of *Lagarodus* might have existed in the northern hemisphere, but this was based on the description of a lateral tooth from Svalbard. The parasymphysial teeth of Greenland, on the other hand, fit perfectly the ones of *Lagarodus specularis,* and as no lateral teeth have yet been found in Greenland, the presence of this putative second species there cannot be tested for the time being.

Lebedev (2008) attributed the family Lagarodontidae to elasmobranchs rather than to euchondrocephals, but at the same time pointed out similarities with both orodontiforms and eugeneodontiforms, which are enchondrocephals (Ginter *et al.* 2010). We therefore follow a more conventional point of view and maintain this family in the Subclass Euchondrocephali, pending a more detailed analysis of the phylogenetic affinities of this family.

Class Osteichthyes Huxley 1880

Actinopterygii Klein 1885

Actinopterygii indet.
Fig. 6

Material. Several isolated teeth (>50), including NHMD 189725.

Description. NHMD 189725 is 1.7 mm high with a conical, slightly sigmoidal shape. The acrodine cap is smooth and represents 22% of the total height of the tooth. The ganoine covering the shaft of the tooth is ornamented by a dense network of very short, irregular ridges (Fig. 6B).

Comparisons. NHMD 189725 presents a shape and an ornamentation of the ganoine similar to the actinopterygian type D teeth described from the Upper Carboniferous of Brazil by Richter *et al.* (1999), and similar to the teeth of Actinopterygii indet. A described from the Kasimovian of Illinois by Carpenter *et al.* (2011). However a similar pattern of ganoine ornamentation is known as early as the Devonian/Carboniferous boundary (Derycke *et al.* 1995).

Discussion

Very few fossil sharks have until now been described from the Carboniferous of Greenland and only four taxa have been known from isolated teeth and fin spines: *Ctenacanthus* sp. (fin spine), *Petalodus* sp., *Lagarodus* sp. and a cochliodontid or menaspid (Bendix-Almgreen 1976). As for *Adamantina,* it was so far restricted to the Permian in Greenland (Bendix-Almgreen 1993). This is therefore the first record of symmoriiform, protacrodont and hybodont sharks, as well as *Bransonella*, from this part of the world. Although the material recovered so far is not well preserved, some taxa appear to be new: the teeth of the Heslerodidae and Hybodontiformes do not fit any known genera. It suggests a rather high endemicity of this fauna. Furthermore, East Greenland might have

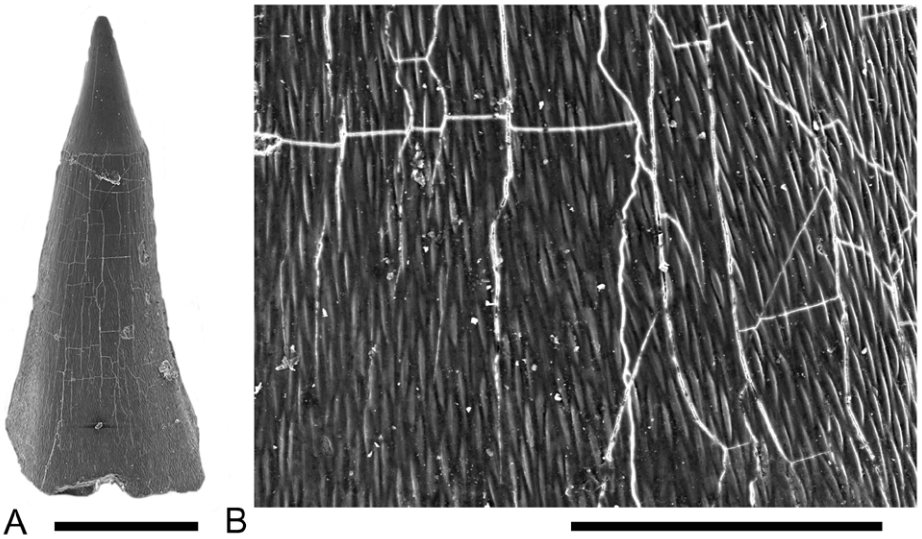

Fig. 6. Actinopterygii indet. NHMD 189725; **A**: tooth in lateral view. **B**: detail of the ornamentation of the ganoine. Scale bars represent 500 μm for **A** and 100 μm for **B**.

been a refuge area for the last protacrodonts as their putative record in Greenland represents their youngest known occurrence.

The fact that *Bransonella* could be represented by three species in Greenland (*B. lingulata, B. nebraskensis* and *B. tridentata)* is a bit surprising, as *B. lingulata* is currently unknown in rocks younger than the Bashkirian (Johnson & Thayer 2009). The poor quality of the material does not allow a deciphering of the relationships of the *Bransonella* teeth from Greenland at species level, but it is nonetheless interesting to note that they represent the most abundant teeth in the assemblage, whereas the genus is unknown from Arctic Russia after the Tournaisian (Ivanov 1999). According to Johnson & Thayer (2009), this genus may have preferred shallow marine water. Its association in Greenland with taxa possessing crushing dentition (*Lagarodus*, indeterminate protacrodont and hybodont) is in accordance with such a hypothesis and fits the overall depositional setting of the Amdrup Land succession (e.g. Stemmerik 2003). The disappearance of *Bransonella* in Arctic Russia after the Tournaisian may therefore be the result of a depositional environment too deep for this genus.

As discussed above, the quality of the material does not allow precise identification of the recovered taxa, and their biostratigraphical value is therefore limited. However, apart from the protacrodont, all of them are compatible with the Moscovian age of the site indicated by the fusulinids (Davydov *et al*. 2001).

Conclusion

The Moscovian Greenlandic fossil fish assemblage comprises several teeth that do not fit any hitherto described taxa. The assemblage encompasses possible new genera belonging to the Heslerodidae and Hybodontiformes, and also provides the youngest record of a protacrodontid. The abundance of *Bransonella* in the assemblage is in stark contrast with contemporaneous records in Arctic Russia, suggesting that the Greenland fauna represents a shallower marine setting.

Acknowledgements

We thank Jakob B. Kristensen and Line Skøtt for help with preparation and sorting. Jakob B. Kristensen also photographed most of the figured specimens under the SEM. We also thank Sten Lennart Jakobsen who took the photographs for Fig. 5 and Lotte Melchior Larsen for her help during the editorial process. The material was collected during GEUS mapping of the area. Finally our most sincere thanks go to the reviewers of the manuscript, Michał Ginter and Alexander Ivanov, who corrected some of our original misidentifications and greatly improved the quality of this work.

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